# B R E V I O R A

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# FOOD-FINDING BY A CAPTIVE PORPOISE (*TURSIOPS TRUNCATUS*)[1]

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Introduction 1
Experimental arrangements 2
Passive location 4
Active or echolocation 4
  Echolocation to determine presence of fish 6
  Echolocation to distinguish between alternate feeding places 7
Passive versus active location 8
Night tests 9
Vision 10
Discussion 12
Acknowledgments 14
References 14

## INTRODUCTION

It soon appears on acquaintance with porpoises that these animals are well endowed with hearing and sight, and that they use both these senses in their normal environment. A captive *Tursiops truncatus* was confronted with the problem of finding unfamiliar food under varying and sometimes rather complicated circumstances, all unlike the normal hunting of his previous wild free existence. Experiments to find out which sense was relied on most and in what ways it was most useful have shown a wide and not unexpected variation in a single individual. Like man, the animal used all the clues he could get. Sometimes he listened, sometimes he looked, and sometimes he was so busy doing whatever he had last done that he missed perfectly obvious clues.

[1] Contribution No. 832 from the Woods Hole Oceanographic Institution.

Although there was such variation in his responses to similar circumstances that many experiments produced conflicting evidence, there was a certain pattern which makes possible a number of conclusions. When he was finding his food he was most eager, swift, and accurate in coming to the sound of a slap on the water. When he had no such clue he would find the fish, evidently by echolocation, if it was in a region where he expected to find food. His final searching for the fish was by eye, though he could not clearly distinguish his preferred butterfish from other offerings. His willingness to use clues, almost we might say his ability to notice them, depended on his memory and other psychological factors as well as hunger.

## EXPERIMENTAL ARRANGEMENTS

Our laboratory on an island at Woods Hole was a pond 34 m. long, 23 m. wide, and 2.5 m. deep, cut off from the sea by a stony beach about 30 m. wide. Our subject was an old bull *Tursiops truncatus*, 203.6 kg. in weight and 267 cm. long, brought here from Florida especially for this experiment. Some injury had damaged his right eye, which we never observed him using, and towards the end of our work his left eye started to cloud over. Whatever the damage was, it did not affect his hearing, which was sharply directional. Temperamentally, he differed from our earlier subject (Lawrence and Schevill 1954), being bold and aggressive, and for this reason was often seen at the surface. Puzzling situations near at hand often caused him to thrust his head above the water, or ''souse out'' in this way to look, and when further off he would ''pitchpole'' straight up for a third or more of his length. He learned fast, and while his evident preference for doing as he pleased would make any formal analysis of his responses rather meaningless, this independence gave a much more varied and accurate picture of his inclinations and abilities than we could have obtained otherwise. Since he preferred going hungry to being forced into situations he disliked, the tests we devised were as simple as were consistent with getting reliable answers. Under these circumstances, it soon became clear that in many cases failure on his part to respond was due not to inadequacy of his senses, but to lack of hunger, temporary unwillingness to approach the feeder, or some other non-sensory reason.

The porpoise was ordinarily fed from a punt 3.6 m. long moored against the bank, usually at right angles, but sometimes parallel to it. In some experiments a small dinghy served as a second feeding station. The position of the feeder in the boat varied. The porpoise was fed dead butterfish (*Poronotus triacanthus*) about 8 to 23 cm. long, held in the water by hand, and was called by an acoustic signal made by slapping the water, or by hammer strokes on a partially immersed iron pipe, or by tones (ranging usually between 500 and 30,000 cycles per second) from an audio oscillator through an underwater sound projector; the pipe and oscillator signals were always remote from the feeding station.

Most of our work was done during daylight, so that we could watch where the animal was and how he responded under different conditions. It was not difficult to keep track of him because he frequently showed at the surface. Because porpoises see well both above and under water, we had to be sure than an apparently acoustic response was not in reality visual. This was the easier because his constant swimming kept the water stirred up and very murky. Transparency by Secchi disk from the surface was rarely as great as 70 cm. and often less than 45 cm.; the very unusual maximum was 85 cm. on 19 September. At 11 o'clock on a typical sunny day measurements made by diving after dark-adaptation gave a Secchi disk reading of 23 cm. from the diving mask at a depth of 2.4 m., and 61 cm. at the surafce. Underwater visibility will scarcely exceed the Secchi disk reading, and will be appreciably less for less bright objects.

This, and observations of the porpoise's behavior when he was finding fish by eye, led us to believe that we are conservative in saying that through the water he could not possibly have discerned with any clarity objects as much as 1 m. away from him. As a further check we repeated most of our tests at night.

We selected the pond because of its great freedom from noise-making animals; the beach protected us from most of the noises of the sea outside. Our listening gear included an AX58C Rochelle salt crystal hydrophone and a WHOI sound level meter (Suitcase), and was sensitive enough to pick up very plainly the noise of fine beach sand strewed into the water 20 m. from the hydrophone.

## PASSIVE LOCATION

One of the most conspicuous traits of our porpoise was the accuracy and confidence with which he promptly made his way to the place where the water had been slapped. There was no uncertainty or hesitation in his response to such a signal; no matter where he was in the pond, he always came with alacrity when he was thus called unless he was not hungry or there were other obvious psychological reasons for his refusing to do so. While failure to reward response to a remote signal often made him ignore subsequent calls, this was never the case with a slap on the surface. As often as we repeated the slap he would return quickly, though we never called him more than four or five times in succession without giving him a fish.

Not only was he prompt in his response to this slap, but, when conditioned to it, he chose it in preference to other clues. If (as described on p. 8) a fish was slapped in one place and held in the water in another, he would choose to go to the place of the sound instead of to the fish, until he learned this clue was unreliable. His apparent reliance on this signal alone sometimes led him to miss a nearby fish entirely.

The porpoise's hearing was sharply directional and his estimates of range (distance) were very close, as is shown by his repeatedly homing directly on a single slap (with no fish in the water) to well within 20 cm. from ranges often as great as 20 to 25 m. through turbid waters and without coming up to look on the way.

## ACTIVE OR ECHOLOCATION

The evidence that our porpoise was echolocating his fish was accumulated over eleven weeks of close observation of his behavior, when an increasing knowledge of what to expect from him under different circumstances made it possible to understand and to check his various capabilities with a fair degree of accuracy.

Early in our work we noticed that our porpoise usually made a characteristic sequence of "creaks" as he came in for a fish, and that in the last meter or so these sounds were matched to horizontal movements of his head. By "creaks" we mean a series

of impulsive clicks made at widely varying repetition rates (from less than 10 to more than 400 per second), the slower ones sounding like knocks and the faster ones like snarls or whines. They have also been called ''barks'', ''snores'', ''rusty hinge'', or ''rasping and grating sounds,'' etc., by various authors, such as McBride and Hebb 1948, Kritzler 1952, and Wood 1954, and have been heard from several odontocetes. Some acoustic details of *Tursiops* calls have been given by Kellogg, Kohler, and Morris 1953. The other common odontocete sound, the whistle-like squeal, was evidently not employed in echolocation, and appears to be primarily communcative. The acoustic details of these sounds will be reported elsewhere.

Before long we noticed that when he was creaking he almost always swam directly to a fish held quietly in the water. When he was not creaking he would not do so. Though this suggested echolocation rather persuasively, we had to be sure that we were not inadvertently giving him other clues and that he was not using sight. His remarkably good hearing and his evident reliance on passive auditory clues made it especially important to make sure he was not coming because he heard us put a fish in water. Very occasionally it seemed highly likely this was just what he was doing, though we ourselves could never detect any sounds, even with our extremely sensitive listening gear. Responses at these few times were discounted. At other times when we were doubtful, we checked his behavior by dipping fish or fingers in and out or dabbling at the surface. This almost never brought him, nor could we get him to come unsignaled to a fish's nose in the water, even though he was coming accurately to a whole fish. Repeated checks also eliminated movements in the boat or the position of the feeder as clues.

The possibility that he was using sight to guide him to a fish had also to be investigated, and we did this in two ways. First of all we devised a series of daytime experiments which, because of the murkiness of the water (see Secchi disk readings), eliminated any possibility that he was using vision to locate his fish from a distance. These experiments are described in some detail below. After we had learned how he reacted to these different situations we repeated the tests at night, with similar results, which are also described below.

Two rather different sets of circumstances stimulated him to rely on echolocation alone in finding his food. Sometimes he used this means to discover whether or not a fish was waiting for him, and sometimes this was the way he distinguished between alternate feeding places.

### Echolocation to Determine Presence of Fish

His reliance on echolocation to tell him whether or not a fish was waiting showed in a number of ways. Often, in the absence of an expected signal, he would circle the pond, creaking only as he passed the feeding station. This was anywhere from 1 to 5 meters away, and occasionally farther. If a fish were in the water as he passed, he would turn and swim directly to it; if there were no fish he would go on by. If a fish were slipped as silently as possible (and we believe inaudibly) into the water after he had passed when he was starting to circle away, he would usually turn and come back. We tried this many times on seven different days. Of these the first is especially significant. It was early in our work and was our first attempt to bring him to a fish without a signal, he being then conditioned to come only to the slap of a fish on the water. At first, although he passed nearby creaking, he did not come to the fish, but later that morning he was attracted some of the time. Five days later we tried again, and he had apparently learned not to wait for a signal. By now he would come in for a fish held silently in the water if he was creaking as he passed by; his decision to come on in seemed usually to be made at a distance of less than 5 but occasionally as much as 15 m. This was repeated a number of times during the next four days, and again two months later.

Our evidence that the porpoise was not seeing the fish before deciding to swim to it was partly his excessive distance when he turned toward it and partly the fact that he often had his bad eye towards the punt as he passed.

As well as using echolocation to find fish when he suspected fish should be available, he also used this means to confirm the reliability of a signal. While he almost never refused to come to the sound of a fish slapped on the water, various circumstances on several occasions made him uncertain about other signals. Early in his training he learned that an oscillator note or pipe-banging in various parts of the pond meant that he would get a

fish at the feeding station, and, like our earlier porpoise, on being signaled with no fish in the water, he would make his way to the proper place to get it. Sometimes, however, he ignored the remote signal until there was a fish in the water as well. With this to convince him he would come unhesitatingly. This reaction was especially clear on four occasions when we had made changes which he did not like in the feeding station. These were all times when he was in good health and hungry, and the remote signal was one we knew he could hear. Until he was accustomed to the new arrangement, no matter how often we called, he always waited till there was a fish in the water before responding to the signal. The first time we had to signal six times with a fish in the water before he began to come on signal only. The other three occasions, at a much later date, were at successive feedings on two days. The first morning it took twelve fish, that afternoon three, and the following morning seven before he would come with no fish in the water. At these times he was creaking as he swam and for the most part responded to the signal by starting towards the feeding station, but with no fish in the water he usually turned away at $2\frac{1}{2}$ meters or more, though sometimes he circled as near as a meter and a quarter. When he was thus relying on echolocation to tell him of the presence of a fish, he rarely troubled to look above the surface. Later, when he was coming on the remote signal with no fish held in, he often soused out of the water on the way in, eyeing the situation from a distance of ten or more meters.

His ability to arrive at a fish he could not see was further demonstrated one afternoon when his left eye failed. At that time, on a remote signal, he repeatedly swam directly to fish held anywhere over a $5\frac{1}{2}$ m. radius.

## Echolocation to Distinguish Between Alternate Feeding Places

To test his use of echolocation, two feeders slapped fish simultaneously on opposite sides of the punt and then one held a fish in the water while the other held a hand out over the water as if feeding. The distance between slaps was about 2 m., and a net projecting 2.5 m. from the end of the punt and hanging to the bottom of the pond prevented the porpoise from circling close

to investigate by eye. We alternated feeding in irregular fashion and the feeders often exchanged places in order to eliminate any other clues. The first time we tried this he came to the correct side 24 times and the wrong side 11, the next time he made 45 correct responses and 13 wrong. His behavior was similar on both occasions. He never ignored a summons and always came directly and fast, creaking as he approached deep. The Secchi disk reading was 61 cm., and he was at the very least 2.5 m. from the fish when he had to decide which side of the net to go. In contrast to his behavior with a remote signal, he made no optical checks on the way in, though sometimes when feeding was slow he pitchpoled out, looking at us. We cannot say how often his wrong responses were caused by the net interfering with his sound patterns. We suspected this on some occasions, while other errors probably are evidence that his echolocation was not perfect.

## PASSIVE VERSUS ACTIVE LOCATION

Experiments to find out what kinds of clues were most successful or preferred produced interesting results. One rather simple but very instructive one, here called the A-B experiment, consisted of slapping at A and putting a fish in the water at B or vice versa, with the distance between A and B farther than he could see. This, with minor variations, we tried many times on each of fifteen different occasions, and though his responses varied, they made a very neat pattern. The first time we tried it, and when we returned to it after a period of other work, he would always swim, creaking, directly to the point of slap, search diligently there, and usually swim away unrewarded. If, in leaving, he found the fish, he would thereafter search at the point of slap and then swim directly to the fish no matter how we varied the relation of these two places to each other. Finally, it was possible to destroy his confidence in the slap as a worthwhile clue, and then for the most part he would go directly to the fish. When he swam directly to the fish there was no possibility that memory could have guided him, because the fish might have been anywhere over a six meter stretch. Nor could vision have helped, because he was never nearer than 6½ meters when we signaled, and usually a great deal farther away. When he

looked first at the point of slap and then went on to find the fish, not pausing on the way, the distance between the two places (minimum 1.3 m., usually more, sometimes as much as 5.2 m.) seemed to preclude the possibility of his being guided by sight, the more so because in this secondary finding of a fish it made no apparent difference whether he approached with his bad or his good eye towards it.

In one variation of the A-B experiment we fixed the points 2 m. apart. If we slapped at A with the fish in the water at B or vice versa, he went directly to the fish; if we slapped with no fish in the water, he searched at the point of slap but never investigated the alternate place as he left unrewarded; if we let him search at the point of slap and then eased a fish quietly into the water at the other place, he would immedately go to it. On a number of other occasions we tried this third modification, varying the place where we put the fish, and he always creaked his way to it. This is not entirely conclusive, as there is a small but unlikely possibility that he might have heard the fish put in, though our efforts to check this led us to believe that this was not passive location (cf. below, p. 11).

## NIGHT TESTS

All of the experiments described above were carried out during the day. We also tried most of these same experiments on dark nights and found the results closely paralleled our daytime observations. On two nights when we tried to get him to take fish unsignaled, he came, apparently directly, making about ten successful runs each time, though he sometimes swam past, creaking, without coming in, and sometimes appeared to search near the fish without taking it. On two other nights we tried the A-B experiment, the first time feeding ten fish which he readily found, though it was too dark for us to see if he made a preliminary search at the point of slap. During the second and more prolonged A-B experiment he repeatedly came to the fish, not the point of slap, especially when he came from far down the pond. Occasionally he searched first at point of slap, and twice he missed the fish entirely. The last night feeding was partly from the dinghy in the middle of the pond. Two slaps informed him that fish were to be had in the vicinity; thereafter

on remote signal he came directly and accurately seven times in a row to a fish held anywhere in a radius of 6 m. Later, when we fed from the punt, he responded to the correct side 6 times, to the wrong side 2, and did not respond at all 2 other times.

## VISION

While sound was important to our animal, we have good evidence that he relied greatly on vision as well, both above and beneath the surface of the water. A bad if not completely blind right eye made him left-sided in his approach to things he wished to see. This was a convenient check when we could not see his eye rolled towards what interested him.

When on arrival from Florida he was dumped into the pond, his first check of his new surroundings was optical. As soon as he hit the water he swam off fast and silently, sousing high out of the water and blowing frequently, with his good eye towards the shore. It was three minutes before we heard him utter a single sound, and nearly two minutes more before he spoke up as loudly and persistently as he did for most of the rest of his stay. It was hard not to think that he was looking over his new surroundings, perhaps searching for a break in the beach. His obvious awareness of things on the shore showed in many ways. During his first two weeks in the pond there were often clusters of people working at different places along the bank. At such times he often blew near them, rolling a little on his right side so that his left eye cleared the surface. Soon he took his surroundings more for granted and his inspections of the shore were less frequent, though he quickly noticed changes. Possibly also with the passage of three or four weeks he became more accustomed to his blind eye; at all events he rolled more often on an even keel, and without bringing his good eye out of the water.

While this kind of check on his surroundings was not important in helping him find his food, it did have a bearing on his behavior at feeding time. Too many people on the bank near the feeding station made him shy, and he would come in deep and depart hastily. The presence of someone in the boat from which we fed aroused his interest, and he would blow nearby, looking. Sometimes it even seemed as if he reacted differently to different feeders.

When we actually called him to eat with the well-understood slap of a fish on the water, he rarely troubled to make an optical check on the way in as he did with a remote signal, but swam directly from wherever he was, to collect his morsel. At other times when he was less sure of the summons, or when we were slow sending signals, he rolled high, looking towards the feeder, or soused out to see what was going on. On occasions when he was more than ordinarily curious, he would pitchpole out of water as far as his flippers, with his good eye looking ventrad towards us.

In addition to keeping track of things above the water, under ordinary circumstances he relied on vision to a great extent in his final accurate taking of a fish from the feeder. Often we could see his eye rolled forward towards the fish. As with our earlier animal, space permitting he would turn over on his side when close, and in the eleven weeks we fed him he only once took a fish with his right eye up. When he lingered at the end of the boat waiting for a fish it was always with the left eye up. When we fed him in a sort of narrow stall 1.2 m. wide so that he did not roll over as he approached, he swung his head from side to side farther to the right than to the left, so that his left eye was in position to scan both sides of the stall as well as the end of the punt.

Fish put in on his blind side or above his head did not attract his attention unless they were splashed. Fish put in nearby and directly in front of him he also took in more fumbling fashion, and on at least two occasions actually bumped into them before seizing them. On the other hand, anything within his range of vision quickly caught his attention. When a fish was moved 15 cm. or so above the water he would follow it with his eye and when it was held lower would put his snout out to snatch it.

Repeatedly, we found a difference in his fish-taking when visibility was especially poor or he himself not seeing well. This usually meant that he would begin his search farther from the fish, nodding his head more widely as he approached slowly, and would be more hesitant about taking the fish, sometimes fumbling and dropping it. A few times, when the fish were small, he missed them entirely. This was true not only when the water was murky, but also when we held the fish deep.

These indications that vision is important in his ultimate locat-

ing of the fish were borne out by his behavior on two separate occasions when the salinity in the pond was down and the water dirty. At these times it appeared that his left eye also was not seeing well. On the first occasion, for three days his fish-finding was less accurate and his search wider than was usual. Once he even bit at the corner of the punt, though the fish was less than 50 cm. away. The other occasion was one afternoon when his left eye failed; then, he approached with it shut, and would lie left side up at the end of the punt, not noticing the fish when it was moved above the surface, but coming to grab it clumsily when it was put in the water. Once when he swam past a fish in the water, he worked his way back to it slowly with very exaggerated head noddings and took the fish awkwardly deep in his mouth. Though his sight recovered after this, he never seemed to see out of his left eye as well as in the beginning. A whitish spot began to form and he would partly close his eye against a low sun, whether because it hurt or dazzled was impossible to tell. At these times his fish-taking was again less accurate, and contrasted with a greater ease when the sun was not shining directly in his eye.

While taking the fish was easier if he could rely on seeing it, he apparently could not discriminate between objects very well. Squid and flattened tin cans don't resemble butterfish much, but even after he had found out he did not like the first two he repeatedly took them in his mouth when they were offered instead of fish. In the same way he would bite at floating vegetation near the boat, at bits of rope, or even at a rusty pail. Size seemed easier for him to tell, and he not infrequently appeared to inspect and then leave small butterfish, about which he was not enthusiastic.

## DISCUSSION

In this study we took a gregarious free-ranging animal that in nature is almost always found at least in small groups and often in immense herds, and placed it in solitary confinement. Whereas wild porpoises hunt live food that occurs in schools, ours was obliged to take single dead fish from the hand. Moreover, the single fish was usually close to a boat or a bank, instead of in the more open water to which wild *Tursiops* are accustomed.

Perhaps the most striking result of our work is the great variation observed in the way our single animal sought his food. His primary reliance on passive auditory clues could have been due to the small size of his target and to the confused echo patterns in the pond. Nevertheless, evidence accumulated that he often echolocated the food we offered him, thus supporting the widespread supposition (for example, Kellogg, Kohler, and Morris 1953) that this was how cetaceans hunted. The sounds the porpoise made at these times were faint; indeed, only the very loudest were audible to a submerged man, and, in fact, were picked up by our sensitive listening gear only because we at last had a porpoise in a really quiet place. Thus we learned that the supposed taciturnity of solitary porpoises (Lawrence and Schevill 1954, pp. 229-231) is rather a relative matter; it appears that they merely speak very softly. The noisy listening conditions of our previous experiment had led us into error when we reported (op. cit., p. 229) ''the complete absence'' of evidence for echolocation although we cited some, unrecognized, at the bottom of page 227.[1] The only evidence we had been aware of was in McBride's posthumous note (in press) on net avoidance (what our porpoise taught us about this will be reported in another paper).

To demonstrate whether an animal is using echolocation, the most definite way is to show that acoustic intereference affects performance. Thus Griffin and Galambos (1941) and Griffin (1953) by deafening bats and nocturnal birds showed that these animals then collided with obstacles that, undeafened, they had avoided. It is of course necessary to make sure that other senses, such as smell (evidently not available to cetaceans) or sight, have been excluded. Furthermore, it must be shown that sounds suitable for echolocation are produced. This last point is abundantly proved for porpoises (e.g., Wood 1952, 1954). The role of sight in our porpoise's food-finding has been discussed under Vision. We did not deafen our animal or interfere with his sound production.

Therefore, our evidence for echolocation by the porpoise is essentially that he consistently found fish when we could convince ourselves that no other clue (sight or sound not made by the porpoise himself) was available.

[1] On page 414 of an article published while this paper was in press, Griffin (1956. Hearing and acoustic orientation in marine animals. Deep-Sea Research, *3*, Suppl. (1955), pp. 406-417) suggests that just such an improved signal-to-noise ratio might reveal evidence of echolocation by porpoises.

The porpoise's performance seemed poorer on targets behind him, particularly at the longer ranges. In general, the creaks with the higher repetition rate were heard at the shorter ranges, but this orderly arrangement was usually confused, perhaps because of additional targets. At close range the creaks were timed to a horizontal sweeping of the head (nodding when on his side). These observations may be interpreted as indicating directionality, presumably in his sound production. We have not investigated this arresting possibility further, except to consider that perhaps the pneumatic cephalic sinuses may modify the radiation of sound from the larynx.

Echolocation was evidently not a perfect method for our porpoise. Perhaps the fault lay in the special conditions in the pond, where the presence of multiple reflections from the stones in the banks and bottom must have confused the echoes. The primary target was a small fish; behind it was the punt, and behind that was the shore. We noticed that when being fed from the small dinghy (with so much less boat in the water to return an echo), he ordinarily came right to the fish with less hesitation than when feeding at the punt. These are indications that echolocation did not give him clear and unequivocal information (human users of this technique will sympathize).

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